

Intra- and inter-specific interactions of foraging American oystercatchers on an oyster bed

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Abstract: We compared the rates of intraspecific and interspecific kleptoparasitism of foraging American oystercatchers (*Haematopus palliatus*) on a commercial oyster (*Crassostrea virginica*) bed during two seasons and between 1979 and 1995. In 1979 most conspecific kleptoparasites were immature oystercatchers and victims were adults. Both intra- and inter-specific parasitism were more common in 1979 than in 1994 or 1995. Kleptoparasitism by conspecifics was more common than by gulls (*Larus argentatus*, *L. marinus*) but was not density dependent. Gulls primarily kleptoparasitized oystercatchers foraging on mussels (*Geukensia demissa*), with their longer handling times. Kleptoparasitism by gulls increased as the number of gulls on the oyster bed increased, and the presence of gulls significantly depressed intake rates and sizes of mussels taken by oystercatchers during autumn. Oystercatchers ate smaller oysters in autumn than in winter in both the presence and absence of gulls. The presence of conspecific and gull kleptoparasites changed the oystercatchers' relative preference for oysters over mussels in their diet. The presence of gulls only partly explained the oystercatchers' lower rates of intake of oysters in autumn than in winter.

Résumé : Nous avons comparé la fréquence du cleptoparasitisme intraspécifique et celle du cleptoparasitisme interspécifique subis par des Huitriers d'Amérique (*Haematopus palliatus*) dans une huître commerciale (*Crassostrea virginica*) en deux saisons, et entre 1979 et 1995. En 1979, la plupart des cleptoparasites étaient des huitriers immatures et les victimes, des huitriers adultes. Les deux types de cleptoparasitisme ont été plus fréquents en 1979 qu'en 1994 ou 1995. Le cleptoparasitisme par des oiseaux de la même espèce était plus fréquent que celui opéré par des goélands (*Larus argentatus*, *L. marinus*) et le cleptoparasitisme intraspécifique n'était pas relié à la densité. Les goélands volaient surtout les proies des huitriers lorsque ceux-ci se nourrissaient de moules (*Geukensia demissa*), proies plus longues à manipuler. Le cleptoparasitisme opéré par les goélands était plus fréquent lorsque ceux-ci étaient plus nombreux dans l'huître et la présence des goélands diminuait significativement les taux d'ingestion et la taille des moules consommées par les huitriers à l'automne. Les huitriers consommaient des huîtres plus petites à l'automne qu'en hiver, en présence ou en l'absence des goélands. La présence de cleptoparasites conspécifiques et de goélands a modifié la préférence relative pour les huîtres plutôt que pour les moules chez les huitriers. La présence de goélands n'explique que partiellement les taux d'ingestion plus faibles en automne qu'en hiver chez les huitriers se nourrissant d'huîtres.

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Introduction

Interference, defined as the decline in the per capita rate of intake of prey when predator density rises, occurs because the presence of other predators interferes with feeding (Sutherland and Koene 1982). As the density of European oystercatchers (*Haematopus ostralegus*) feeding on mussels increased, their ingestion rate decreased (Zwarts and Drent 1981; Sutherland and Koene 1982; Ens and Goss-Custard 1984; Goss-Custard and Durell 1987a; Goss-Custard et al. 1995a). This interference was associated with an increase in rates of aggression that occurred as bird density rose (Vines 1980). The amount by which the ingestion rate of an individual European oystercatcher was depressed as oystercatcher density increased depended on the bird's aggressiveness (Ens

and Goss-Custard 1984; Goss-Custard et al. 1995a, 1995b) and also on its foraging efficiency and feeding method (Goss-Custard 1987b). The potential maximum rate at which a bird can feed is assumed to be set by its intake rate in the absence of competitors (Vine 1980). In winter, the density of European oystercatchers on a mud flat in England was high enough on neap tides for interference to depress average intake rates of juveniles and adults to 59 and 64% of their potential maximum, respectively (Goss-Custard and Durell 1987b).

Intra- and inter-specific kleptoparasites (food thieves) use the time and energy investment of others to reduce their costs of obtaining food (Thompson 1986). Kleptoparasitism is a major feeding strategy of several gull species (Kallander 1977; Hoffman et al. 1981; Thompson 1986). Throughout the winter in Mauritania, lesser black-backed gulls (*Larus fuscus*) and grey plovers (*Pluvialis squatarola*) took more than half the cockle flesh captured by European oystercatchers (Swennen 1990).

In this paper we examine the effects of long-term and seasonal decreases in food supply (Tuckwell and Nol 1997) on the frequency of intra- and inter-specific interactions of American oystercatchers at a commercial oyster (*Crassostrea virginica*) bed in coastal Virginia, U.S.A. We use data from an older study (Cadman 1980) as the basis for the long-

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term comparison. In a previous study (Tuckwell and Nol 1997) we found that oystercatchers increased their intake rate and ate larger oysters in winter than in autumn. In this study we attempt to understand these seasonal changes in relation to the frequency of kleptoparasitism on foraging oystercatchers. In the previous study we also found that handling times for oysters were considerably shorter than those for ribbed mussels (*Geukensia demissa*), but that mussels were eaten more frequently in autumn than in winter (Tuckwell and Nol 1997), and we predicted that gulls would preferentially kleptoparasitize individuals foraging on mussels (Steele and Hockey 1995). As immature oystercatchers do not have the ability to forage as efficiently as adults, and therefore may rely on kleptoparasitism to increase their daily energy intake (Cadman 1980; Goss-Custard and Durell 1987b), we also predicted that the most frequent intraspecific interactions, both in the long-term data set and in recent field seasons, would take the form of immature birds kleptoparasitizing adults.

Study sites and methods

Study sites

This study was conducted during three time periods: October–December 1993, October–December 1994, and 7–15 February 1995 at the Queen Sound oyster bed, located 5 km west of the island of Chincoteague, Virginia (37°56'N, 75°28'W; Tuckwell and Nol 1997). Salt marshes, channels, bays, mud flats, sand flats, and oyster beds characterize the area. The dominant vegetation of the salt marshes includes salt hay (*Spartina patens*), smooth cordgrass (*Spartina alterniflora*), and saltwort (*Salicornia* sp.). The Queen Sound oyster bed is manmade, consisting of American oysters, which were last seeded in the summer of 1993, and ribbed mussels, which grow wild. A full description of the study area is given in Tuckwell and Nol (1997).

Observations of kleptoparasitism

We counted the oystercatchers and gulls (*Larus argentatus*, *L. marinus*) each hour on the bed and during every kleptoparasitic attack for each day during autumn 1993 (29 observation hours in total), autumn 1994 (67 h), and winter 1995 (27 h). For each bird, one of us (J.T.) recorded the prey species and size chosen by the oystercatcher. Mean ingestion rate ($\text{mL} \cdot 5 \text{ min}^{-1}$ of observation) and volume of oysters or mussels were calculated as per Tuckwell and Nol (1997). We compared intake rates and sizes of oysters taken between autumn and winter and in the presence and absence of gulls.

During each kleptoparasitic interaction we also recorded the species and ages of thief and host and whether the attempt was successful. An adult American oystercatcher has bright yellow irides, light pink legs, and a bright reddish orange bill. An immature oystercatcher in its first or second year was distinguished from an adult by its pale yellow irides, greyish legs, and pale orange bill with a black tip (Cadman 1980).

Statistical analysis

We tested whether intake rates were influenced by the number of conspecifics or gulls, using Kendall's rank correlation coefficient (Sokal and Rohlf 1995). We used stepwise logistic regression (Kleinbaum 1992) to determine if the presence of gulls or oystercatchers influenced prey choice by oystercatchers. In these analyses we had to adjust for the effects of tide on prey choice, as we found earlier that during the rising tide, oystercatchers choose a greater proportion of mussels than during the falling tide because of the ability of mussels to use anaerobic respiration (Tuckwell and Nol

1997). All data were tested for normality, and if they were non-normal, nonparametric tests were applied.

Results

Descriptions of interactions

In intraspecific encounters, an oystercatcher was often attacked by another oystercatcher as soon as it showed the typical prying movements associated with opening an oyster or mussel. In almost all cases, the host gave up its food immediately to the thief and continued foraging. Only rarely was the food defended by the host and the thief rebuffed.

Gulls were seen scattered among oystercatchers on the oyster bed. The number of gulls on the bed varied throughout the day as individuals flew to and from other locations surrounding the study area. During a kleptoparasitic attack a gull would take flight and head for an oystercatcher, which would take off, followed closely by the gull. Some oystercatchers gave up their prey, dropping it as soon as the gull started the chase. Oystercatchers could fly faster than the gulls but were usually outmanoeuvred on their return to the oyster bed and forced to give up their prey. The oystercatchers were often attacked before they could open the bivalve and therefore the gull made its attempt too early and was unsuccessful.

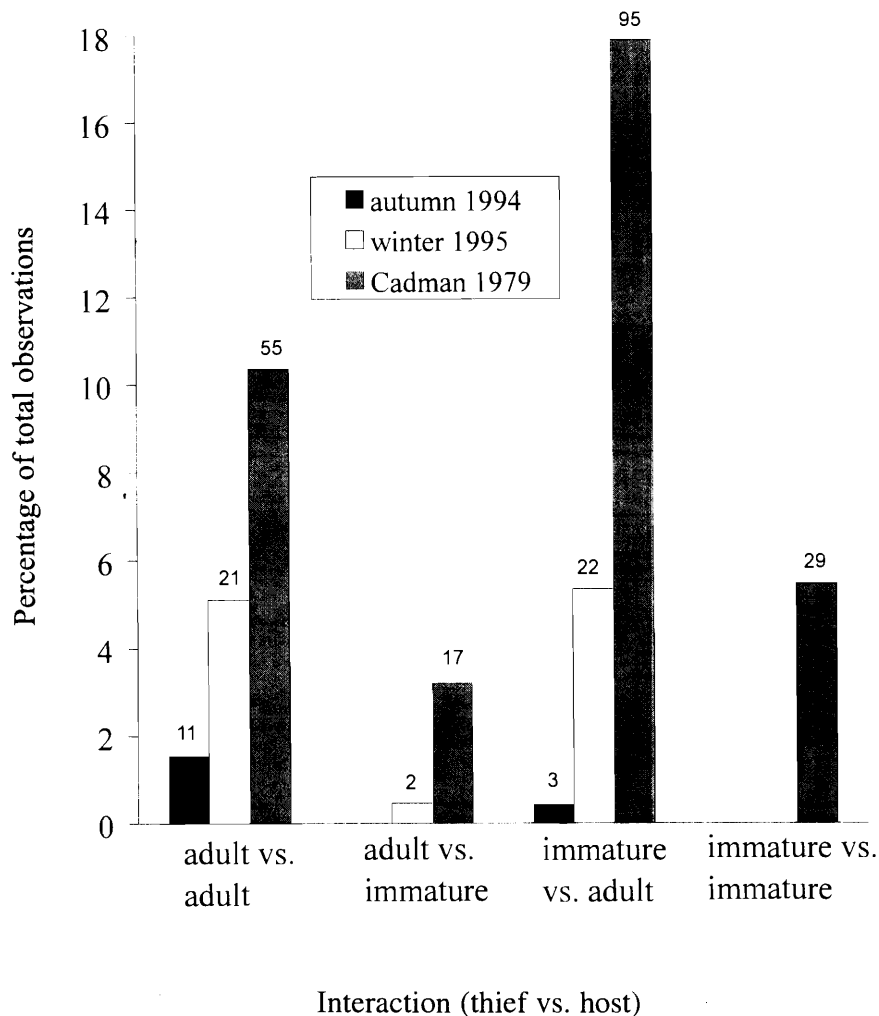
Rates of kleptoparasitism

Intraspecific kleptoparasitism occurred at over twice the frequency in winter 1979 than in winter 1995 (196 of 335 (36.9%) versus 55 of 500 (11.0%) foraging attempts; $G = 104.58$, $P < 0.0001$). In 1979, immature oystercatchers made up the majority of thieves, whereas in 1994 and 1995, thieves were about equally split between adults and immatures (Fig. 1). These numbers could not be compared statistically because the birds were not marked and we did not know what proportion of birds were not thieves. Seasonally, intraspecific kleptoparasitism occurred more frequently in winter than in autumn (55 of 500 (11.0%) versus 14 of 706 (2.0%) observations from 1993 and 1994; $G = 44.1$, $P < 0.0001$; Fig. 1).

The average numbers of gulls per hour on the Queen Sound oyster bed did not differ between autumn 1994 and winter 1995 (3.32 ± 0.50 versus 3.02 ± 0.53 ($\bar{x} \pm \text{SE}$); $t_s = 0.25$, $df = 37$, $P = 0.80$). The maximum number of gulls observed during autumn 1994 was 22, whereas the maximum observed during winter 1995 was 10. Gulls kleptoparasitized oystercatchers significantly more frequently in autumn than in winter (56 of 720 foraging attempts (7.8%) versus 10 of 431 (2.3%); $G = 14.86$, $P < 0.001$). The success rate for gull kleptoparasites was marginally lower in winter than in autumn (4 successes of 10 attempts versus 16 successes of 56 attempts; Fisher's exact test, $P = 0.06$). Of the 66 kleptoparasitism attempts (successful and unsuccessful) over both seasons, 59 (89.4%) were to steal mussels, while only 7 (10.6%) were to steal oysters.

Intraspecific kleptoparasitism did not increase as a function of the number of oystercatchers on the oyster beds (range of $r^2 = 0.02$ – 0.26 , all nonsignificant for each year and food item). By contrast, interspecific kleptoparasitism occurred significantly more frequently as a function of the number of gulls present ($r^2 = 0.28$, $P = 0.02$; Fig. 2).

Fig. 1. Frequency of intraspecific kleptoparasitism (percentage of total foraging observations) at the study site in autumn 1994, winter 1995, and winter 1979. Data from winter 1979 are from Cadman (1980). Numbers above the bars indicate the total number of observations.



Kleptoparasitism, prey choice, sizes, and ingestion rates

The logistic regression model (Kleinbaum 1992) used to determine if oystercatcher flock size influenced the oystercatchers' prey choice at the Queen Sound oyster bed (using data from 1993–1995; Tuckwell 1996) produced an odds ratio of 1.2792. This represents a 27.92% ($\chi^2 = 15.2$, $P < 0.0001$) increase in the odds of oystercatchers choosing an oyster over a mussel in the presence of one additional oystercatcher, when adjusted for the effects of tide and the flock of gulls present at the Queen Sound bed. We also ran the analysis holding tide and the number of oystercatchers constant, and found a stronger odds ratio (i.e., a stronger effect of gulls than conspecifics on prey choice, 1.3535 or 35.35%, although the difference was not statistically significant ($\chi^2 = 3.60$, $P = 0.058$)). A stepwise multiple logistic regression with both numbers of conspecifics and numbers of gulls indicated that the effect of conspecifics on prey choice was greater than the effects of gulls.

When intake rates were compared between seasons we found a significantly higher intake rate in winter than in autumn in the presence of gulls but not in their absence, although mean intake rates were still lower in autumn (Table 1). When we did the same two comparisons with the

volume of oysters, we found that oystercatchers ate larger oysters in winter in both the presence and absence of gulls. The lower intake rates in autumn in the presence of gulls is attributable to oystercatchers consuming smaller oysters in autumn than in winter, but also to more time elapsing between successive prey captures (i.e., longer search times), resulting in lower intake rates. We could not do the same analysis with and without oystercatchers because of very small sample sizes in the absence of conspecifics.

We found that the volume of mussels chosen by oystercatchers declined with increasing gull numbers (Fig. 3a). We found the same trend for rates of intake of mussels: with larger numbers of gulls on the beds the intake rate for mussels declined significantly (Fig. 3b). This analysis was only done on the data collected in autumn because oystercatchers ate very few mussels in winter.

Discussion

Our previous study unveiled a paradox: American oystercatchers ate larger oysters, had higher intake rates, and spent less time finding the oysters in winter than in autumn (Tuckwell and Nol 1997), although declining prey avail-

Fig. 2. Relationship between the number of gulls present at the oyster bed during autumn 1994 (■) and winter 1995 (□) and the number of interspecific kleptoparasitic attempts (successful and unsuccessful combined).

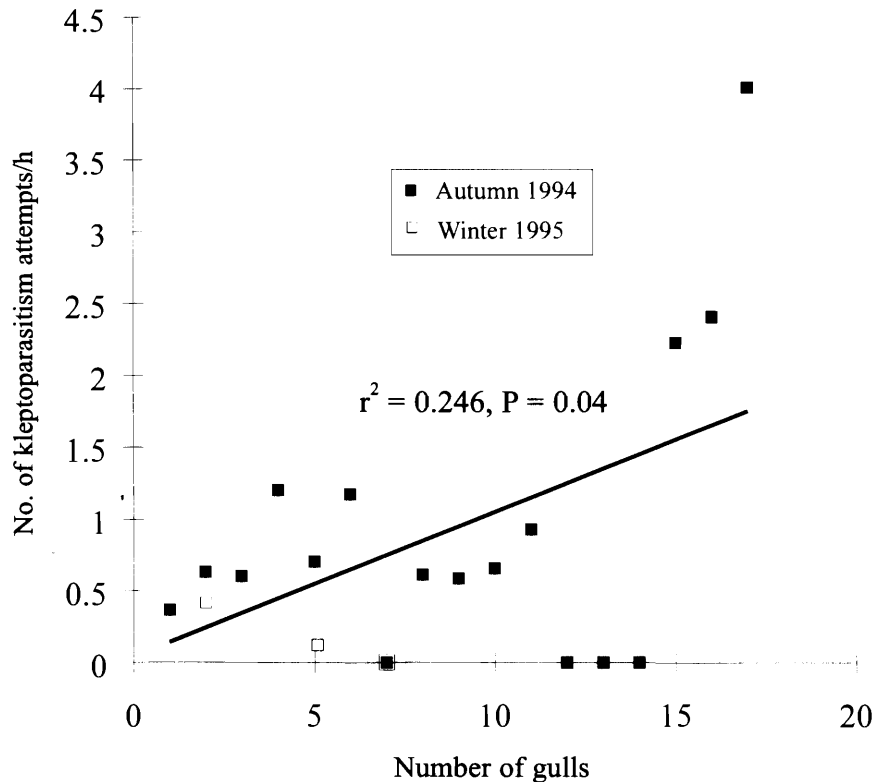


Table 1. Comparison of intake rates and volumes of oysters between autumn (1994) and winter (1995) with and without the presence of gulls.

		Autumn 1994		Winter 1995		t_s^*	P
	Gulls	Mean	N	Mean	N		
Intake rate (mL/5 min)	Without	7.41 (1.60)	19	10.78 (2.47)	14	1.44	0.15
	With	6.02 (0.76)	85	11.63 (0.96)	115	3.82	0.0001
Volume (mL)	Without	2.32 (0.24)	18	4.83 (0.50)	19	3.99	<0.0001
	With	2.44 (0.15)	101	3.52 (0.15)	145	4.94	<0.0001

Note: Values in parentheses are standard errors. N is the number of individuals.

*Significance was tested with Wilcoxon's rank-sum test.

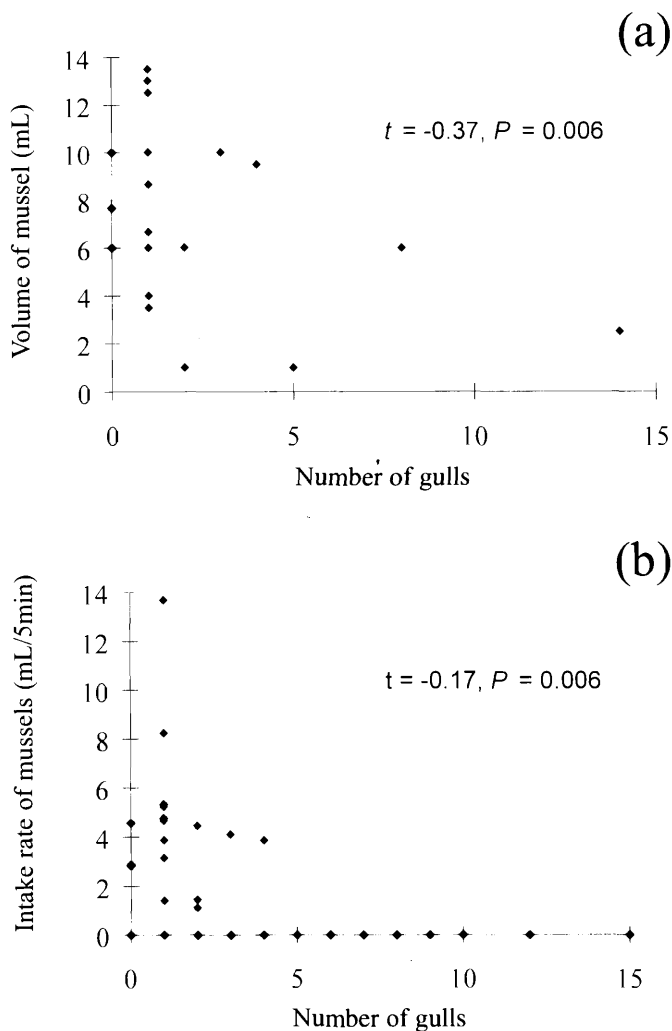
ability in winter should have predicted lower intake rates (Maron and Myers 1985). The results of the present study suggest only a partial explanation for this paradox. We found mussels on the oyster bed only in autumn, and these were apparently chosen primarily because few other prey were available during the rising tide (Tuckwell and Nol 1997). Despite the long handling times of mussels relative to oysters, their flesh was substantial (greater than the flesh of oysters) and probably provided considerable energy during these tidal periods.

One of the disadvantages of foraging on mussels was that gulls (and conspecifics) kleptoparasitized the oystercatchers during foraging attempts. The attempt resulted in wasted energy for the gulls, as the oystercatcher often flew away to evade the kleptoparasite. Conspecific parasitism, by contrast, did not generally result in flight. Gulls were on the bed in both seasons but kleptoparasitized oystercatchers only in

autumn while the oystercatchers foraged on mussels, with their longer handling times. Intake rates of oystercatchers foraging on oysters in both the presence and absence of gulls were lower in autumn than in winter, although only significantly lower with gulls present, suggesting a partial effect of gulls on intake rates, probably through an increase in the time between successive prey captures due to disruption or harassment by gulls.

Our analysis showed that oystercatchers ate smaller oysters in autumn than in winter regardless of the presence of gulls. Therefore we still do not understand why the oysters chosen by oystercatchers were smaller in autumn than in winter, although in winter larger oysters make sense from an energy perspective (Goss-Custard and Durell 1987a). In winter, when there were very few mussels on the bed, it was no longer worth the effort for gulls to parasitize oystercatchers, and oystercatchers could reduce their search time

Fig. 3. Sizes of mussels consumed by oystercatchers ($N = 28$) (a) and intake rates ($N = 126$) (b) in autumn 1994 in the presence of gull flocks of different sizes.



and enhance their intake rates. Changes in the reproductive status and hence the potential food value of oysters from autumn to winter (Goss-Custard and Durell 1987a) do not explain the shift in prey size because oysters reproduce in summer in the Chincoteague area (M. Luckenbach, Virginia Institute of Marine Sciences, personal communication).

European oystercatchers did not experience interference while foraging on small prey items (Goss-Custard and Durell 1987a). It is possible that smaller oysters were selected by American oystercatchers in autumn as a tactic for reducing handling time to avoid becoming the victims of kleptoparasitism. We think this is unlikely, however, because handling times for large oysters were still brief relative to those for mussels, and generally an oystercatcher could swallow a large oyster without interruption. It is possible that smaller oysters were being chosen by oystercatchers in autumn for energy and (or) nutrition reasons (Boates and Goss-Custard 1988) unrelated to changes in the reproductive status of the oysters.

Both the size of mussels chosen and the intake rate of mussels were affected by the number of gulls present on the bed: greater numbers of gulls led to fewer and smaller mussels

being chosen. This result concurs with those of Kallander (1977), who reported that both lapwings (*Vanellus vanellus*) and golden plovers (*Pluvialis apricaria*) chose smaller worms in the presence of black-headed gulls (*L. ridibundus*) than in their absence.

The level of intraspecific kleptoparasitism was higher in winter than in autumn, but in neither season was it density dependent. There was also no relationship between the size of mussels or oysters chosen or intake rates of these prey items and the number of oystercatchers present. This result suggests that particular individuals were specialized as kleptoparasites (Brockmann and Barnard 1979), although in detailed studies of European oystercatchers, specialization was not found (Goss-Custard et al. 1982). We also found that oystercatchers were more likely to choose oysters over mussels when more conspecifics were present. Therefore, the presence of conspecifics affected one aspect of prey choice, whereas the presence of gulls affected a number of aspects of the foraging behaviour of oystercatchers. Goss-Custard et al. (1995a, 1995b) found that individual aggressiveness influenced the ability of oystercatchers to counteract the effects of intraspecific kleptoparasitism. We did not observe much aggression between individuals, but the rate of kleptoparasitism was quite low (11% at its maximum) compared with rates reported for European oystercatchers.

Cadman (1980) observed a significantly higher rate of intraspecific kleptoparasitism than we did, which was due, in part, to the greater number of immature birds recorded foraging at the Queen Sound oyster bed in winter 1979. The reason why so few immature birds were recorded during this study is unknown. Either nesting success in the region was low in the years prior to our observations or immatures chose to winter elsewhere. Intraspecific kleptoparasitism was probably also more prevalent in 1979 because more oystercatchers foraged on the Queen Sound bed (Tuckwell and Nol 1997), which increased the probability of intraspecific interactions. The apparently larger number of interactions between immatures (as thieves) and adults (as victims) in 1979 than in 1995 was probably also a result of the greater proportion of immatures on the oyster bed in 1979.

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